POLLINATION ECOLOGY AS AN ASSAY FOR ECOSYSTEMIC ORGANIZATION: CONVERGENT EVOLUTION IN CHILE AND CALIFORNIA

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SUMMARY

Diversity and feeding specialization (with/without niche overlap) of pollinating insects was examined at 0.5 km^2 sites along transects including analagous physiognomic plant communities in California and Chile. Though climates at the analogous community sites are similar, plant diversity ($\underline{H}$ and species count) patterns differ due to the prevalence of fire in the California sclerophyll scrub. Treating the distinct floras of the fire cycle additively, plant diversities of similar communities compared intercontinentally are more similar than within-country diversity comparisons of adjacent communities. The diversity of all taxonomic groups of pollinators manifests consistently greater intercontinental analogue similarity than compared to different physiognomic communities within the same country. All pollinator groups are more diverse in California due to the larger area and the presence of more diverse refugia from Pleistocene glaciation. Similar percentages of the resident flora of analogue communities rely upon wind, insect and self-pollination, whereas adjacent but different communities may differ markedly; the same analogous relations hold for the component pollinator groups with the exception of syrphid flies. Utilization strategies exhibit emphasis on generalists (by species) in maritimal and Mediterranean scrub environments; emphasis on generalists (by individuals) in the Mediterranean scrub; emphasis on feeding specialists (by species and individuals) in the desert; and emphasis on very few species of abundant generalist feeders in the cool forest and maritime environments of both countries. Results are commensurate with the hypothesis that climate controls the phenological presentation of floral resources and that these in turn determine the abundance and diversity of floral herbivores in optimized patterns irrespective of a completely distinct evolutionary heritage within the two continents.

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INTRODUCTION

As many plant ecologists (most notably Holdridge in 1947) have demonstrated, the physiognomy of any climax biome is determined in large measure by a few preeminent features of the climatic regime: rainfall, temperature and evapotranspiration. In regions with a Mediterranean climate, plants are especially affected by such climatic features, in particular by the water stress imposed by high temperatures and lack of appreciable summer precipitation. More than a century and a half ago, Alexander von Humboldt was impressed by the similarity of vegetation types in widely separated regions of the world, but only recently has convergent evolution in regions of Mediterranean climates been investigated in a holistic manner.

The investigations reported in this paper, which were conducted under the auspices of the International Biological Program, are an analysis of species packing at the interface between flowering plants and the flower-feeding herbivores which often act as the agents of cross-pollination. These studies were designed to distinguish between the physiological effects of climate and the historical influence of the taxonomic composition of the flora and fauna in determining the structure of an ecosystem. Ecosystem structure is assessed in terms of the species diversity of component guilds and the patterns of their competitive interactions.

In order to distinguish between the variables of taxonomic composition and climatic similarity, an Analysis of Variance design was employed utilizing two parallel transects of research sites under very similar climatic conditions but 7,500 km apart and comprised of very different faunistic and floristic lineages (Thrower and Kummerow, 1977). With the exception of a few pest and weedy species associated with commerce, there is little taxonomic similarity between the two regions in question below the family level (Raven, 1963; Mooney, 1975, 1977; Moldenke, 1976). Within the transect in each country on the other hand, the sites subject to differing climatic regimens share the same taxonomic lineages.

If the effects of climate significantly outweigh the taxonomic component within a community and if convergent evolution has been occurring, the well-documented similarity of community physiognomy should be indicative of pervasive similarities extending through the phenology, physiology and diversity patterns of resident floras; it should be reflected indirectly as well in the totality of resource utilization strategies of animal groups. Convergence at the physiological level within the Mediterranean floras of Chile and California has been shown to be the result of selection for similar physiological strategies (Mooney and Dunn, 1970; Mooney _et al_., 1970; Mooney, 1972, 1977). This observation signifies that the resource base is sufficiently similar in the two hemispheres to provide a basis for comparative analysis of food web relations.

If climate acts additionally to limit the total amount and the temporal presentation of floral resources in arid and Mediterranean regions, then optimization theory (Schoener, 1971; Cody, 1974) would predict strong convergence in the total biomass, the diversity and the structure of the flower-feeders' food web. Such convergence should be evident in a pattern of similarity between analogous intercontinental sites which must exceed the levels of similarity within the transect design of each continent. If similar patterns of species packing of flower herbivores which function as pollinators are achieved in intercontinental analogous sites, then presumably a similar percentage of the floras would be relegated to genetically compatible selfing or to wind pollination.

These testable hypotheses necessarily assume a similar duration of evolutionary development in the two hemispheres and a similar pattern of recent resource utilization by man. Although the situations in Chile and California do differ in some details, most of the null assumptions are in fact fulfilled or at least the situations are closely parallel. The discrepancies which do exist will be discussed as they become pertinent.

METHODS

a) Site Selection

Site selection for this integrated research project was established with the aid of a number of investigators having a wide variety of expertise. Great care was exercised to match the sites as closely as possible on the basis of the available climatic, topographic and land-use information. Perfect climatic matches, considering the number of pertinent variables, clearly would be statistically highly improbable. The sites chosen, described briefly below and in considerable detail in Thrower and Bradbury (1977) and Mooney (1977) are remarkably similar. All share "mediterranean" climatic regimes in that precipitation falls almost exclusively during the relatively cool seasons.

Mediterranean Sclerophyll Scrub

California, San Diego County, Echo Valley near Descanso: altitude ca. 1,000 m; annual precipitation 32 cm; mature chaparral with little understory, last recorded fire in 1950 (25,600 hectares); no grazing and little human disturbance; dominant cover Ceanothus, Arctostaphylos, Adenostoma and Quercus.

California, San Diego County, Japatul Valley near Descanso: altitude ca. 1,000 m; annual precipitation 32 cm; chaparral burned severely in 1970, investigations carried out during two years subsequent to fire; burn the largest (total 70,000 hectares; Phillips, 1971) in recent history of the region, nearest source area nearly 7 km distant; site located in close proximity to Echo Valley; entire cover fire-sprouted annuals and geophytes.

Chile, Santiago/Valparaíso Provinces, Fundo Santa Laura on the Cuesta la Dormida: altitude ca. 900 m; annual precipitation ca. 52 cm; the least disturbed extensive region of mature matorral with any sort of access to electricity and automobile in central Chile; light to moderate grazing by llama, burro and cattle; patrolled for 10 years to prohibit charcoal gathering and goat grazing; dominant cover Lithraea, Quillaja, Trevoa, Retanilla, Cereus, Cryptocarya and Satureja; investigations mostly completed before central laboratory was established and hence areas studied extensively were directly accessible from the main Cuesta and hence a bit more disturbed than regions studied by other workers.

Coastal Scrub

California, San Diego County, Torrey Pines State Park: altitude sea level to 100 m; annual precipitation 27 cm (Felton, 1965); the only region available for 50-150 km in either direction with a semblance of native flora and fauna; region honeycombed with footpaths, annual visitation rate is 700,000 people; remarkably undisturbed portions studied; local excellent botanical society floral listing available; island-like isolation of present system and extreme abundance of Apis mellifera are differences between the California and Chile sites; fauna and flora assumed to be depauperate representation of pre-colonial condition; dominant plants Rhus, Dudleya, Cneoridium, Eriophyllum and Mesembryanthemum.

Chile, Valparaíso/Aconcagua Provinces, Papudo: altitude sea level to 100 m; annual precipitation 30 cm; localized regions of relatively undisturbed community between the resort towns of Papudo, Zapallar and Maitencillo; though portions of region are severely overgrazed and extensively developed, regions furthermost from settlements appear undisturbed, with only occasional sightings of Apis; dominant plants Baccharis, Puya, Bahia, Fuchsia, Lobelia, Cereus, Calandrinia and Mesembryanthemum.

Montane Forest Community

California, San Diego County, Mount Laguna: altitude 1,700-1,900 m; annual precipitation ca. 60 cm; freezing temperatures and snow in winter; extensive stand of Quercus-Pinus woodland with little shrub cover but a well-developed understory; rather undisturbed, but grazed by cattle.

Chile, Santiago/Valparaíso Provinces, approaching cima Cerro El Roble: altitude 1,700-2,000 m; annual precipitation ca. 70 cm; freezing temperatures and snow in winter; mountaintop island Nothofagus forest; heavily grazed and timbered; though an official IBP site, the region was regarded as too disturbed to directly compare resource allocation patterns; observed and censused nevertheless.

Chile, Angol Province, Parque Nacional Nahuelbuta (37° S): well-preserved and extensive remnant of Nothofagus and Araucaria rain forest; analogous to Big Basin State Park (38° N), Santa Cruz County, California, a Sequoia rain forest community type. (quantitative sampling not undertaken)

Desert Scrub Community

California, Imperial County, Ocotillo: altitude 100-200 m; annual precipitation "average" less than 10 cm; studied in year of extensive spring rain and subsequent two years when there was virtually none, though supposedly characterized by occasional summer rains as well, only one storm left any noticeable moisture over a circular area with radius of 75 m (Pectis papposa and its pollinator Perdita albovittata were the only signs of life) during these three years; surrounding slopes with succulent vegetation observed wherever rainfall pattern permitted; extensive flat lower bajadas of Larrea, Franseria, Fouquieria, Agave and Opuntia.

Chile, Coquimbo Province, vicinity of Miña El Tofo:

altitude 750 m; annual precipitation less than 10 cm; partially, though not completely, sheltered from effects of coastal fog by seaward ridge of transverse mountains; studied during one year of exceptional rainfall and one year of minimal rain; though not as extensively studied as other sites, large data base available from local bee biologist, R. Wagenknecht; dominant plants Cereus, Eulychnia, Opuntia, Proustia, Balbisia and Aristolochia.

Coastal Community

Chile, Coquimbo Province, Cerro Potrerillo near Cd. Coquimbo: succulent desert community; altitude sea level to 100 m; coastal thick fog every day throughout October and November; ground cover both years of study exceptionally diverse and lush; both years with plagues of larval Sphyngidae; dominant plants Cereus, Eulychnia, Oxalis gigantea, Heliotropium and Bahia.

California, Marin County, Point Reyes: fog shrouded coastal dunes, strand and scrub vegetation at 38° N latitude; dominant plants Mesembryanthemum, Lupinus, Cakile and Ammophila (Moldenke, 1975, 1976b).

Alpine Community

Frequent research excursions were made to the vicinity of Farellones and Portillo in the high Cordillera (3,000-4,000 m) in central Chile for the purposes of comparing the communities with high altitude central Sierra Nevada, California (see Moldenke, 1971, 1975, 1976b). Quantitative censusing was not undertaken in the Chilean sites.

b) Censusing and Resource Allocation

Methods employed in plant censusing, herbivore censusing, and determining the relative resource utilization of the herbivores are described in detail in Moldenke (1971, 1975). The raw data from all sites are available from the author in complete form in Moldenke and Neff (1974b).

It should be noted that for purposes of this study, biomass is not measured directly but is assumed to be proportional to an estimate based on the volume of floral and insect tissue of each species censused. Floral "biomass" is thus not equivalent to animal "biomass" nor is it likely that single biomass "units" of different taxa measured in this way would be exactly equivalent if translated to grams, calories or more typical conventional currency. Despite such obvious shortcomings, I feel the method is justified both by its simplicity and by the striking differences in amounts of "biomass" involved. More precise estimations of "biomass" are not likely to change the general patterns observed.

RESULTS AND DISCUSSION

a) Diversity of the Flora

The similarity evident in the over-all pattern of the broad-leaved sclerophyll evergreen scrub vegetation and emphasis on annual plant speciation in Chile and California is discernable as well in the pattern of occurrence of the different physiological strategies within the environmental mosaic (Mooney, 1972, 1977). For example, similar sets of growth patterns, leaf size and shape, succulence and therophyte drought avoidance strategies tend to be characteristic of certain slope faces (Parsons, 1973, 1976). These correlations or morphological characteristics of the disjunct resident floras consistently evidence greater similarity between analogous community types in opposing hemispheres than between any two adjacent community types within either hemisphere (Parsons and Moldenke, 1975).

Since the climatic parameters and the adaptations of the flora of Chile and California are similar, species diversity of the dominant plants in the broad-leaved evergreen sclerophyll communities should approximate the same values in regions of similar extent chosen for their similar geologic heterogeneity (MacArthur and Wilson, 1967). However, three environmental and historical dissimilarities between the two regions indicate that within the framework of predicted similarity (when compared to physiognomically distinct neighboring community types), species diversity values would be lower in Chile _in toto_, but higher per unit area than in California.

1) The size of the land mass subject to a Mediterranean climate in Chile is less than that of California (California = ca. 240,000 km^2; Chile = ca. 100,000 km^2). Since the geographical heterogeneity of the two regions is remarkably comparable, the direct proportionality between species number and area would predict a more diverse California flora (MacArthur and Wilson, 1967).

2) The refugia available for the flora during the recurrent pluvial and interpluvial climatic fluctuations of the Quaternary were much more restricted in

Table 1. Plant abundance and diversity

	Censused Individuals 1000m^2	Censused Species 1000m^2	Total Species Count (0.5 km^2)	H Diversity of Abundance	Floral Biomass	H Diversity of Floral Biomass
California						
Coastal Scrub	79,899	83	140	2.15	2,755	2.82
Mediterranean Scrub Burn	43,236	85	157	2.89	2,625	2.46
Mediterranean Scrub	2,636	44) 103*	72) 205*	2.79	8,969	2.11
Deciduous Forest	85,713	55	84	2.44	49,337	0.65
Desert Scrub	41,110	39	140	1.66	2,220	1.53
Chile						
Coastal Scrub	110,055	131	154	2.46	16,508	2.71
Mediterranean Scrub	270,853	108	158	1.12	10,302	2.84
Coastal Succulent Scrub	20,388	94	105	3.40	45,423	1.66
Desert Scrub	79,019	76	80	1.03	2,508	2.71

South America (Vuilleumier, 1971). Each subsequent climatic reversal should therefore have had a resultant progressive decrease in the species diversity of Chile.

3) The California chaparral is a fire-adapted ecosystem. It cycles, with a natural pre-colonial periodicity of about eight years (Aschmann, 1959), between a dominant shrub community with essentially no understory and a dense cover of fire-sprouted annual and geophyte species with little photosynthetic shrub cover. There does not appear to be a similarly intense fire-associated evolutionary phenomenon in Chile (Parsons and Moldenke, 1975; Mooney, 1977). Since these pre-colonial fires were presumably very limited in geographic extent (compared to present fires), a mosaic of differing successional seres apparently existed within very close proximity facilitating refuging for both floral and faunistic elements, allowing all elements to persist within a relatively circumscribed region. These seral elements are sometimes combined where appropriate in the analysis which follows.

The Chilean matorral site with 108 species censused is very similar to the combined censuses of mature and burned California chaparral with a total of 103 species (Table 1). The Chilean matorral with the tremendous inequality of numbers between shrubs and annual plants is, however, much less diverse in terms of the information measure <u>H</u> (Lloyd and Ghelardi, 1964) than is the mature California chaparral even though in terms of the absolute number of species it encompasses, the Chilean site is slightly richer than the combined burned and mature sites of California.

Although the total extent of matorral vegetation in Chile contains as many woody Mediterranean scrub species as the total chaparral of California (Chile = 246: 217 trees and shrubs, 29 succulents[1]; California = 249: 217 shrubs and trees, 32 succulents[2]), thirty species of shrubs occur in the 1,000 m^2 censused in Chile, whereas only nineteen occur within the California census. The

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[1] Data supplied by Prof. Otto Zöllner, Universidad Catolica, Valparaíso, Chile.

[2] Data collated from Munz, 1955.

TABLE 1. Total species count within total extent of community (less than 1 km^2) of Chilean deciduous forest is 23. Personal data supplemented by Carter (1973); this low value is undoubtedly a result of present overgrazing and recent intense lumbering.

*Summation of total species count in either burned or unburned Mediterranean scrub vegetation.

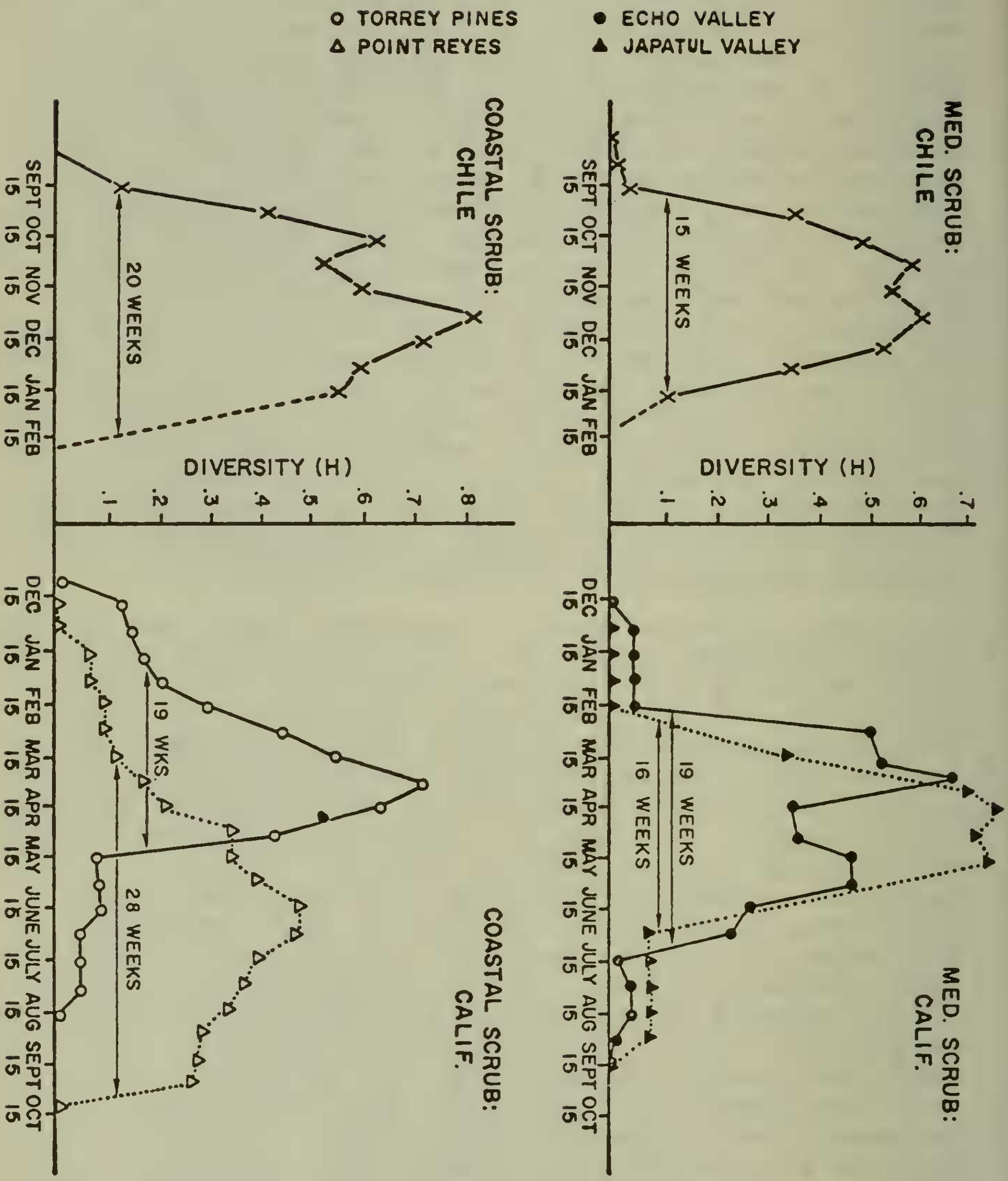
Table 2. Pollinator vs. Floral Biomass.

	Pollinator Biomass	Floral Biomass	Ratio P/F Biomass
California			
Coastal Scrub	664	2,725	.24
Mediterranean Scrub	3,012	8,969	.33
Desert Scrub	1,530	2,220	.70
Chile			
Coastal Scrub	946	16,508	.06
Mediterranean Scrub	2,549	10,302	.24
Desert Scrub	700	2,508	.28
Coastal Desert	370	45,423	< .01
Northern California			
Coastal Scrub	2,531	10,628	.23

decreased local species count of dominant shrub species within a small region (1-2 km^2) in California may reflect the rapid response by r-strategist shrubs to the periodic catastrophic destruction of the climax canopy caused by fires in California. Total species count (including ephemeral therophytes and geophytes) is high in these mosaics of continual reinvasion; once the shrub cover reestablishes, a monoculture of the original or most aggressive shrub colonist often results. This low diversity is probably characteristic of the California community in its pre-colonial state (DiCastri and Mooney, 1973). In Chile, the few remaining regions of relatively undisturbed natural scrub are characterized by the relatively high diversity levels censused in this study. In contrast, the majority of the matorral scrub vegetation type in Chile is presently heavily exploited by man, particularly by heavy selective cutting for firewood and intense overgrazing by goats (Parsons, 1973). As documented by Harper (1969), continued application of such selective pressures results in a community dominated by very few species of plants (in Chile: Acacia caven, Satureja gilliesii and Lithraea caustica).

Total species count of censused plant taxa is high in Mediterranean scrub ($\bar{x} = 105$) and coastal scrub ($\bar{x} = 107$) and drops off noticeably in forest ($\bar{x} = 39$) and desert ($\bar{x} = 57$) of both continents (Table 1). The noticeable discrepancy between desert censuses may be due to the maritimal location of the Chilean site with a more predictable incidence of precipitation and fog condensation. The species counts of the mature California montane forest community and the deserts of both hemispheres are conspicuously less rich than other California communities censused by the same method ($\bar{x} = 87$; Moldenke 1975). Measures of structural diversity have not been utilized in this study because pollinators do not respond to the same cues utilized by other groups (e.g. Cody, 1974). As a general phenomenon, total plant diversity (both species count and information indices) and floral-herbivore diversity have been shown not to be correlated (Moldenke, 1976, 1979). Though conclusive studies are lacking, it appears that pollinator diversity is usually highest in warm arid ecosystems characterized by an abundance of bare ground and little wind regardless of resident plant diversity.

The respective paired sites of Mediterranean scrub and desert scrub show close correspondence (Tables 1 and 2), both in species number and amount of floral biomass. The coastal scrub of Chile provides noticeably more floral biomass than that of California, primarily due to the contributions of three common mass-blooming species, Puya chilensis, Baccharis linearis and B.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MED. SCRUB: CHILE
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concava. The Puya is pollinated by the giant hummingbird (Patagonia gigas) and is structurally analogous to the Agave species of the coast of southern California and Baja California. The Baccharis spp. bloom so very late in the year that I have not had the opportunity of observing their pollinators, but collections by H. Toro (pers. comm.) reveal that they are heavily frequented by halictine bees and various groups of flies; they are the only flower resource available during the very late Chilean summer.

A significant lack of climatic correspondence between the Mediterranean scrub and coastal scrub community comparisons can be seen in Figure 1. While the blooming season in coastal Chile is significantly longer than that of the corresponding Mediterranean scrub (by 4-5 weeks), the blooming season in Torrey Pines is equal to that of the corresponding dominant Echo Valley community. The blooming season further to the north in California is more than twice as long as that of the scrub communities at the same latitude due to the earlier and warmer spring on the coast and to increased precipitation during late spring[3]. This ameliorating influence is not pronounced in southern California since there is not enough moisture during the summer months to permit extensive flowering except at elevations over 1,500 m; rainfall at 38° N is double that at coastal 33° N.[4] The

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[3] Blooming period at Point Reyes is 30 weeks long, that at Stanford is only 12 (Moldenke, 1971, 1974).

[4] Mean annual rainfall: Point Reyes (38° N) = 49 cm; Torrey Pines (33° N) = 27 cm (Felton, 1965).

FIGURE 1. Blooming seasons at Mediterranean and Coastal Scrub sites in Chile and California. Blooming seasons at Torrey Pines, Echo Valley and Papudo are equivalent whereas the blooming season is significantly decreased at Cuesta la Dormida and increased at Point Reyes. The length of the blooming peak is measured by:

$$H = -\sum_{s=1}^{n}(p_s)(l_n\, p_s)$$

N is the total number of plant species (s) in the community; p is the proportion of each species of the total community floral biomass resource. Diversity is used to measure the floral peak rather than species count or simply total flowers available due to the disproportionately large number of species with very few flowers in the earliest spring and the long-lasting mass blooms of one or two species in the fall. Peak blooming season is defined at the 0.1 level of diversity, except for Torrey Pines where inspection reveals that 0.18 is the preferable delimitation.

TABLE 3. Relative abundance of flower-herbivores along Chile/California transects.

	Torrey Pines	Burned Chaparral	Chaparral	Mt. Laguna Forest	Ocotillo Desert	Papudo	Matorral	Potrerillo	Desert
Bees (species)	80	151	171	135	87	64	116	22	29
(individuals)	3,108	6,297	55,749	11,032	9,905	2,918	28,815	475	4,824
(H individuals)	2.82	1.55	2.37	2.01	2.15	1.69	1.79	0.87	1.23
(H relative biomass)	2.13	1.11	2.09	1.59	1.84	1.67	2.12	0.95	0.82
Beetles "	7	16	41	17	24	20	34	11	20
	133	4,024	4,925	3,195	570	2,394	711	869	1,480
	0.18	0.60	0.38	0.58	0.23	1.00	0.11	0.77	0.65
	0.02	-	-	-	-	-	-	0.28	0.48
Lepidoptera "	3	13	15	13	4	4	13	3	3
	68	2,732	2,750	78	14	8	615	7	8
	-	0.40	-	-	-	-	0.10	-	-
	-	-	-	-	-	-	0.16	-	-
Muscoid Flies "	10	11	19	8	5	12	23	6	4
	55	417	140	196	755	48	261	22	9
	-	-	-	-	-	-	-	-	-
	-	0.39	0.40	0.37	-	-	-	-	-
Syrphid Flies "	4	1	6	3	3	12	27	7	3
	15	80	79	180	240	118	15,529	95	115
	-	-	-	-	-	0.11	0.95	0.24	-
	-	-	-	-	-	-	0.77	0.10	-
Wasps "	7	38	31	13	36	3	39	5	29
	69	335	804	63	453	4	505	15	297
	0.10	0.13	-	0.26	0.21	-	-	-	0.19
	-	-	-	-	0.14	-	-	-	0.09
Bee Flies "	7	22	24	16	22	14	28	5	12
	261	4,200	4,989	1,470	640	423	1,865	89	144
	0.30	0.71	0.34	0.34	0.22	0.30	0.20	0.23	0.12
	0.18	0.58	0.44	0.32	-	0.24	0.20	0.16	0.12
Hummingbirds* "	1	2	2	2	1	1	1	1	0
	73	133	187	73	44	55	46	18	0
	-	-	-	-	-	-	-	-	-
	0.36	0.30	0.31	0.30	0.22	0.37	0.22	0.34	-
Total spp.	119	254	309	207	182	130	281	59	100

length of the entire growing season is correspondingly reduced in southern California although this U.S. Weather Bureau statistic does not reflect the summer drought as strikingly as does the observed blooming season.[5] The decreased length of the blooming period is reflected in the reduced quantity of total floral biomass and the diminished abundance of the flower herbivore fauna resident in the Torrey Pines research site (Table 2).

b) Flower-Herbivore Abundance

Significantly larger numbers of species, individuals and biomass of flower-herbivores occur in the Mediterranean scrub (Tables 1 and 3) than in any other community type. Flower-herbivore species count of Mediterranean scrub is three times that of desert in both continents, twice that of coastal scrub in Chile, and four times that of coastal scrub in California. Flower visitor biomass follows a similar pattern to that of species diversity within both continents. Viewed in terms of flower-herbivore individuals, the richness of the chaparral in both countries (particularly California) is greatly augmented by the occurrence of enormous numbers of minute individuals of several flower-visiting species (e.g. _Perdita_, _Panurginus_, _Bibio_ and _Geron_). Although they may facultatively specialize on one species or a related group of plant species, these species are probably inefficient pollen vectors. Their small size, low mobility and habit of visiting flowers in close proximity (usually on the same plant) may render them functional pollen and nectar robbers, since the plants they frequent are genetically self-incompatible.

In the coastal scrub community the flower-herbivore biomass (Table 2) decreases significantly since the maritimal climate decreases flight time for poikilothermous insects by at least two hours a day and commonly prohibits flight for the entire day when fog settles along the coast. The depressing effect of the fog on insect activity relevant to potential pollination is much more severe in Chile, where fog is a much more frequent and prolonged occurrence, than in California. The Humboldt Current, which parallels the Chilean coast

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[5] Growing season: Point Reyes = 361 days; Stanford (37° N) = 307 days; Torrey Pines = 336 days; Echo Valley (33° N) = 216 days (Felton, 1965).

TABLE 3. Flower-Herbivore Abundance.
*Based on individual sightings; all other abundances represent sampling without replacement.

$H = -\sum_{s=1}^{N} (p_i)\ (l_n\ p_i)$ where: N = total species (s) in community; (p_i) = relative abundance of species_i in census.

(colder and closer than the California Current of western North America), exerts its influence along the entire coast. Cerro Potrerillo is almost a true fog desert. Temperatures are so lowered and fog so common that the time favorable for poikilotherm activity is limited to only one hour per day (ca. 2:30-3:30 PM) for the extent of the peak blooming season (1 October to 1 December). The only pollinator activity possible at other times is by large relatively heavy-bodied facultatively homeothermic ("heterothermic"; Heinrich, 1974) hummingbirds, large bees (e.g. Caupolicana, Trichothurgus) and nemestrinid flies. Though minimal rainfall did not permit study of the climatically analogous Baja California coastal succulent sites, the same limitation of activity periods and relative importance of heterothermic flower-herbivores occurs along the coast of northern California.

The efficiency at which floral biomass is utilized within the trophic levels of the community may be approached by the ratio of total flower-visitor biomass supported divided by the total community floral biomass (Table 2). This ratio can only be used to show the general pattern of resource availability, since precise nutritional aspects are not known; there is no real evidence that more pollen or nectar is "wasted" in communities with high floral/animal biomass ratios. This ratio is lowest for the succulent fog desert and reaches a maximal value for the desert communities of both hemispheres. Similar to the situation encountered at Cerro Potrerillo, flower-herbivore activity at Point Reyes is virtually restricted (99 percent of community pollinator biomass) to thermoregulatory heavy-bodied insects. An analogous phenomenon occurs at a similar latitude in Chile, where the single species Bombus dahlbomi assumes the role of the diverse Bombus fauna in California (7 species at Point Reyes). At high latitudes in both continents nearly all the bee pollination occurs through the agency of Bombus in all community types.

In desert communities, the ratios in Table 2 are maximized. In these communities more than half of all species of flower visitors (e.g. beetles, wasps, leps, beeflies) are not bees. Though evidence is growing that these groups are consumers of pollen as adults (Gilbert, 1972; Jack Hall, pers. comm.), it is probable that their increased frequency of floral utilization in deserts reflects more accurately the increasing relative value of nectar in an environment in which moisture is otherwise unavailable to many insect groups. In all other communities studied by the author, by far the largest percentage of visitors to flowers consists of bees which are utilizing pollen as a major food source for themselves and their larvae.

c) Flower-Herbivore Diversity

With the exception of Torrey Pines (see site selection), it is immediately apparent that the California sites are much richer in total flower visitors than their Chilean counterparts (Table 3). This pattern of α-diversity is reflected best within the bees (Apoidea) and in varying degrees in other groups as well. Bees are the group expected to show closest correspondence to floral abundance and diversity patterns.

An analysis of the bee diversity of all Chile (in contrast to only the local diversity of the research sites) and the corresponding region of North America (Baja California to southern Alaska) reveals a total of four times as many species of bees in the Northern Hemisphere (Moldenke, 1976). In the absence of any comprehensive botanical treatment of the Chilean flora, it is not possible to distinguish between the presumed lower total diversity of Chilean plants and the smaller total area as causes of this observed decrease in Chilean bee species.

A similar gradient of bee species diversity exists throughout the diverse biotic realms within each continent, both on the level of point sites and comparisons of the species inhabiting the total expanse of analogous community types. Therefore the flora of the corresponding climatic regions of the opposing hemispheres are faced with similar exigencies in attracting vectors to their flowers. Depending upon altitude and distance from the arid subtropics, a flora may have either a very rich potential vector fauna of both specialists and generalists or only 1/7-1/8 as many taxa, nearly all of which are generalists (Moldenke, 1976).

A significant ratio of potential significance in any community is the number of flower-visiting axa relative to the number of non-anemophilous flowering plant species. This number is, of course, not an absolute indicator of pollinator availability since one "facultative specialist" such as Apis can presumably perform the pollination function of a large number of specialist species. The ratio of bee species[6] to ento-

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[6] With their characteristic morphology and behavior patterns which usually bring them in contact with anthers and stigmata, their high rate of flower visitation per unit time and their densely furry bodies, nonparasitic

mophilous plant species resident within localized regions of Mediterranean scrub, desert and grassland communities is likely to exceed 2.0 (Moldenke, unpublished data); however, in coastal, alpine and boreal forest communities, the ratio may drop to 0.6-0.3 and the flora is generally faced with a severe competition for vectors. The competition between plants for pollinators is especially intense in these latter communities since these regions of low bee diversity are characterized by generalist-feeding opportunist bee species which visit most frequently those plants which offer them the greatest reward per effort expended (Moldenke & Lincoln, 1979). In the Mediterranean and desert scrub communities more than half of the bee taxa are coevolutionarily associated with only one plant taxon. These specialist-feeding bees may afford a predictable source of outcrossing regardless of the identity of sympatric plant species or the fact that many plant taxa serviced by specialist bees are visited under most circumstances by more efficiently pollinating generalist bees.

In contrasting the evolutionary history of the bees of Chile and Pacific North America (Moldenke, 1976), it is clear that both faunas possess relict species of ancient groups of long-standing distribution patterns as well as relatively recent taxonomic groupings actively adapting and speciating in new environments. However, whereas the Pacific North American fauna has received novel evolutionary stocks very frequently from the Neotropics, Nearctic and Palaearctic, the Chilean region has been relatively isolated. Though the species count of Chile is distinctly less than that of Pacific North America, it must be borne in mind that with respect to area, Chile does itself possess one of the most diverse bee faunas in the world. The Pacific North American bee fauna is clearly larger in total species and in the number of distinct genera that seem to have evolved *in situ* or in the closely associated Madro-Tertiary Geoflora region. Sixty-six genera and subgenera inhabiting semi-arid Pacific North America appear to have had an endemic origin; the corresponding number for Chile is only 22. The number of endemic bee genera (33% of the total Chilean bee genera) in Chile is larger than the comparable number in Pacific North America (9%). This higher level of endemicity in Chile is partially attributable to the isolation of Chile by the Atacama Desert

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bees represent the most important pollinator group; in the virtual absence of quantified studies on the vectoring efficiency of groups other than bees, it is impossible to estimate the number that are truly important as pollinators.

and the Andean Cordillera (Moldenke, 1976).

d) Pollination of the Flora

The relative abundances of different groups of flower-visitors is shown in Table 3. Not every insect which visits a flower is an effective pollinator nor is the relative abundance of all species of floral herbivores an index of their relative contribution to outcrossing. In the absence of autecological studies with marked pollen grains on each species of insect observed to utilize flowers as a food resource, my own subjective judgment based on field observation of intrafloral behavior, insect morphology and fidelity to a particular plant species by individuals for short extents of time are the basis of my judgment as to whether any significant pollination may be attributable to a particular species. In this paper no judgments are made as to the quantitative relative efficiency of different species of vectors servicing the same species; all species that on the above grounds are deemed potentially significant vectors are so treated in Tables 4 & 5, for instance. Infrequent but consistent visitation by a bumblebee to a flower in which it usually contacts the reproductive structures weighs equivalently with an abundant syrphid species which feeds heavily upon one particular plant species, but seldom contacts the stigma.

The species count of butterflies and skippers in Chile (ca. 75, pers. comm. H. Toro) is much less than it is in Pacific North America (238; Ehrlich and Ehrlich, 1961; D. MacNeill, pers. comm.), though comparable species diversities are maintained at each of the research sites. In both continents the preferred floral resource of butterflies is the Compositae; on these plants butterflies are often efficient vectors of pollen.

Wasps are abundant in the Mediterranean scrub and desert scrub ecosystems of both hemispheres; along with bees and beeflies (Bombyliidae), they form one of the most diverse floral-herbivore groups. In California the odd "vespoid bees," Pseudomasaris spp. pollen and nectar collecting wasps (Evans, 1966; Malyshev, 1968), are conspicuous elements of the flower visitor community, frequenting flowers of Phacelia (Hydrophyllaceae) and Penstemon (Scrophulariaceae). Gayella, a poorly known genus of this group, is found throughout central Chile; if they have specific floral preferences, they are unknown. The masarid wasps are efficient pollinators, but their more diverse sphecoid and vespoid relatives are significant vectors of pollen only in the desert where they may visit some plant species ignored by other flower visiting groups.

Diverse families of beetles (particularly the Mordellidae, Cerambycidae, Chrysomelidae, Dermestidae, Scarabaeidae, Buprestidae and Melyridae) are frequent visitors of flowers in both continents; however, for both morphological and behavioral reasons they seldom are effective as vectors of the pollen of the plants concerned. The Compositae are a favored resource. A remarkable example of convergent evolution is seen in the case of two abundant beetle pollinators, Nemognatha (Meloidae -- California) and Lichnia (Scarabaeidae -- Chile). Both are equipped with elongate labial palps, which in certain species are considerably longer than the length of their bodies. These probosces appear to be uniquely suited for extracting nectar from the long tubular disc flowers of the Compositae they visit.

Flies, as pollinators, must be subdivided into at least three groups: feeble-flighted Nematocerans, hovering beeflies, short-tongued syrphid and muscoid flies. Each of these groups generally visits a different set of flowers, apparently transfers pollen with widely differing efficiencies, and occurs in different preferred habitat types. The primitive Nematoceran flies appear to be extremely inefficient as vectors of pollen and are typically most abundant in communities characterized by large amounts of shade. Their activity is restricted to moist microhabitats during the early spring of typically more arid associations. Their effect in the regions of this study is expressed as the occasional outcrossing of taxa that normally self-pollinate; this is in contrast to their role in arctic communities, where their relative abundance coupled with the paucity of other pollinator types renders them significant elements in the pollination of the resident floras (Faegri and van der Pijl, 1966; Kevin, 1970). Beeflies (Bombyliidae and the Nemestrinidae [Chile only]) are a diverse and efficient group of pollinators at each of the research sites. Unlike research sites at higher latitudes in each country (Moldenke, 1971, 1975) where only one or two beefly species assume a major role in the pollination ecology of forest communities, along the more arid

TABLE 4. Categories represent actual pollinators documented in study, rather than floral syndromes (i.e. perching short-tongued insect class) à la Knuth and subsequent authors (Faegri and van der Pijl, 1966). % flora = Number of species pollinated by particular mode divided by total species in region. Columns may total to more than 100% since taxa may be efficiently pollinated by more than one pollinator class.

Table 4. Plant pollination syndromes along California transect.

	Torrey Pines Coastal Scrub	Japatul Valley Chaparral Burned	Echo Valley Chaparral	Mount Laguna Oak-Pine Forest	Ocotillo Desert Scrub
Solitary Bees					
# species	37	35	32	33	34
% flora	27%	24%	41%	41%	29%
Specialist Pollen Vectors (bee subset)					
# species	24	18	20	16	24
% flora	18%	12%	29%	20%	21%
Halictine Generalist Bees					
# species	10	8	5	1	2
% flora	7%	5%	7%	1%	2%
Beeflies					
# species	3	11	4	7	2
% flora	2%	7%	6%	9%	2%
Beetles					
# species	4	3	0	3	3
% flora	3%	2%	-	4%	3%
Wasps					
# species	1	8	2	2	5
% flora	1%	5%	3%	3%	4%
Butterflies and Moths					
# species	3	4	1	1	2
% flora	2%	3%	1%	1%	2%
Hoverflies					
# species	3	3	0	0	4
% flora	2%	2%	-	-	4%
Muscoid Flies					
# species	1	1	2	1	3
% flora	1%	1%	3%	1%	3%
Hummingbird					
# species	4	8	10	6	3
% flora	3%	5%	14%	8%	3%
Water					
# species	4	6	0	0	0
% flora	3%	4%	-	-	-
Wind					
# species	21	16	7	16	13
% flora	15%	11%	10%	20%	11%
Selfers (predominantly)					
# species	45	35	6	10	44
% flora	33%	24%	9%	13%	38%
(Obligate Selfers)(subset)					
# species	12	9	1	3	7
% flora	9%	6%	1%	4%	6%

Table 5 Plant pollination syndromes along Chile transect.

	Papudo Coastal Scrub	Fundo Santa Laura Matorral	Cerro Potrerillo Succulent Desert	El Tofo Desert Scrub
Solitary Bees				
# species	33	48	16	27
% flora	22%	53%	16%	36%
Specialist pollen vectors (bee subset)				
# species	7	21	5	17
% flora	5%	23%	5%	23%
Halictine Generalist Bees				
# species	7	13	0	0
% flora	5%	14%	-	-
Beeflies				
# species	7	1	6	7
% flora	5%	1%	6%	9%
Beetles				
# species	6	1	5	3
% flora	5%	1%	5%	4%
Wasps				
# species	1	2	2	4
% flora	1%	2%	2%	5%
Butterflies				
# species	2	3	1	0
% flora	2%	3%	1%	-
Hoverflies				
# species	5	11	4	1
% flora	4%	12%	4%	1%
Muscoid Flies				
# species	6	2	3	3
% flora	5%	2%	3%	4%
Hummingbird				
# species	7	7	4	0
% flora	5%	8%	4%	-
Water				
# species	1	1	2	1
% flora	1%	1%	2%	1%
Wind				
# species	25	19	10	5
% flora	17%	21%	10%	7%
Selfers (predominantly)				
# species	47	27	48	23
% flora	32%	30%	48%	32%
(Obligate selfers) (subset)				
# species	13	3	9	2
% flora	9%	3%	9%	2%

community transects (Table 4) beeflies are diverse and very abundant in all communities.

Although the short-tongued muscoid flies are often more likely to contact anthers and stigmas than the long-tongued beeflies, simple abundance counts commonly overestimate their importance as pollinators due to their low floral visitation rate per unit time. While active foragers such as bees, beeflies or hummingbirds normally spend far less than 30 seconds visiting a particular flower, muscoids commonly spend from 5-10 minutes per flower, but even more extensive periods of time are spent resting on leaves, twigs or stones between subsequent visits. In both countries muscoid flies (particularly the Anthomyiidae in California) are extremely abundant on flowers in high latitudes or high altitudes (Moldenke, 1971, 1975), whereas they are an inconspicuous element in the transects reported herein (Table 3). Along these two transects more than 90 percent of the muscoid diversity is accountable to the Tachinidae, abundant flower visitors parasitic during their larval phase upon diverse insect groups. Tachinids are particularly prevalent as a flower visiting group in the Chilean desert, but scarce in the California deserts where they appear to have been replaced by other parasitic insects (e.g., Bombyliidae, Meloidae); their pronounced vestiture of extremely long setae may act to transfer pollen rather efficiently, but such analytic studies remain to be undertaken.

The hoverflies (Syrphidae) represent the sole noticeable lack of correspondence between the null hypotheses of convergence and actual field conditions. Hoverflies are faunistically diverse in California (E. Schlinger, pers. comm.) but neither abundant nor well-represented at the particular southern California transect sites. Except for the unique situation where one species, <u>Eupeodes</u> <u>volucris</u>, is abundant and a major source of outcrossing for numerous early spring desert annual species (at least during the years of this study), they exert little effect as pollinators within the community. This one species seems to be about the only flower-herbivore able to fly in the very cool and very windy conditions so typical of many of the days in the early spring in the Colorado Desert. In Chile, on the other hand, Syrphidae are very abundant in the Mediterranean scrub, and even more pronouncedly so in the forests and highest altitude matorral of the Cordillera de la Costa and at 3,000-4,000 m in the Andean Cordillera of central Chile. Nowhere in Chile is the syrphid fauna diverse, even though they are oftentimes very conspicuous elements of the flower visitor fauna.

Nearly all of the abundant syrphid species are predators upon the Aphidae as larvae; this facet of pollination ecology apparently is a function of an abundant aphid resource resulting from low levels of aphid predation by groups other than the Syrphidae. In central Chile, there are many species of introduced gregarious aphids which provide a large resource for predators; coccinellid beetles are uncommon in Chile and apparently the syrphid flies have responded to these introduced pest species with noticeably increased abundance (E. Schlinger, pers. comm.). In California, and western North America in general (Moldenke, 1971, 1976b), the primary flower visiting syrphids occur at high elevations and are large-bodied primarily Holarctic groups (e.g. Volucella, Eristalis) that are detritivores and herbivores as larvae, a faunal element conspicuously reduced in central Chile.

The most important single group of pollinators in all sites are the solitary bees. Forty percent of the flora rely upon solitary bees for the movement of pollen in the Mediterranean scrub and forest communities, whereas 25 percent and 27 percent of the flora, respectively, in the coastal and desert communities rely upon this group. The only significant differences between the community analogue comparisons are an increased percentage of the flora utilizing solitary bees and hoverflies in the Chilean matorral and a smaller percentage of obligate selfing and a compensatory increase in the reliance upon beeflies in the Chilean desert scrub.

The diversity and abundance of classes of pollinating agents is not only being monitored by ecologists, it is also being monitored through evolutionary time by the resident floras of California and Chile. The coevolutionary patterns of reliance upon certain insect groups as pollinating agents and the percentage of the flora reduced to genetic self-compatibility and habitual selfing are additional gauges of the relative success of pollinators. The relative percentages of the flora at each research site associated with a particular mode of pollination is shown in Tables 4 and 5. In every case (considering Cerro Potrerillo as a derivative desert community) there is much greater similarity between the analogous community sites in opposing hemispheres than between sites in different communities located along the same transect. The importance of selfing increases from a low level in the forested and chaparral community to a high in the deserts and coastal scrub (see also Moldenke, 1971, 1976b, 1979b). Increased incidence of the annual habit is the primary correlate of selfing as a reproductive strategy. All annual plants are to some extent *r*-strategists, usually finding existence too tenuous when genetically self-incompatible. Thus the vast majority of annuals in both California and Chile (even if locally efficiently pollinated and not scored as selfers in Tables 4 and 5), have evolved the ability to set seed facultatively in the absence of pollinators.

A paucity of all types of floral visitors, let alone the more efficient types of pollinators *per se*, is a chronic feature of maritime environments, where the coolness of the weather markedly decreases the abundance of floral-herbivores. In the desert where pollinators are usually limiting to all but the dominant plants, even during years of large amounts of rainfall and a peak emergence of pollinators, the total extent of the blooming season for annual plants will still be very restricted. An escape from pollinator limitation unavailable to desert annuals is to extend the blooming period of the species. Annual plants along the coast (e.g. *Lasthenia* spp.) may bloom for a period half again that of the same species in the desert and chaparral (6:4 weeks) (Moldenke and Neff, 1974b). Though an equivalently high percentage of the plant species along the coast and in the desert are genetically self-compatible, the most telling characteristic of their pollination ecologies is the observation that more than twice as many species along the coast are obligate selfers (Moldenke, 1976b). Many of the self-compatible species in the desert undoubtedly receive considerable outcrossing during a year of appreciable rainfall.

e) Resource Utilization Strategies

As in all other communities studied, the preponderance of species of flower-herbivores are found in association with 1-3 plant species (Moldenke 1971, 1975, 1979c; Heithaus, 1974). This trend is apparently always true on a local sample basis (Figure 2), even if the rare species are excluded from the tabulation; faunistic lists that deal only with preferred resources across wide geographic extents are however very different in divergent community types (Moldenke, 1976b, 1979).

The most difficult and time-consuming aspect of this study has been the determination of the relative degrees of feeding specialization exhibited by solitary bees along the two transects. Host preference among species of bees ranges from the extreme generalist with virtually catholic tastes to the extreme specialist which restricts its pollen collection to a single plant species; examples of all possible intermediates between these extremes are known. Host specialization among

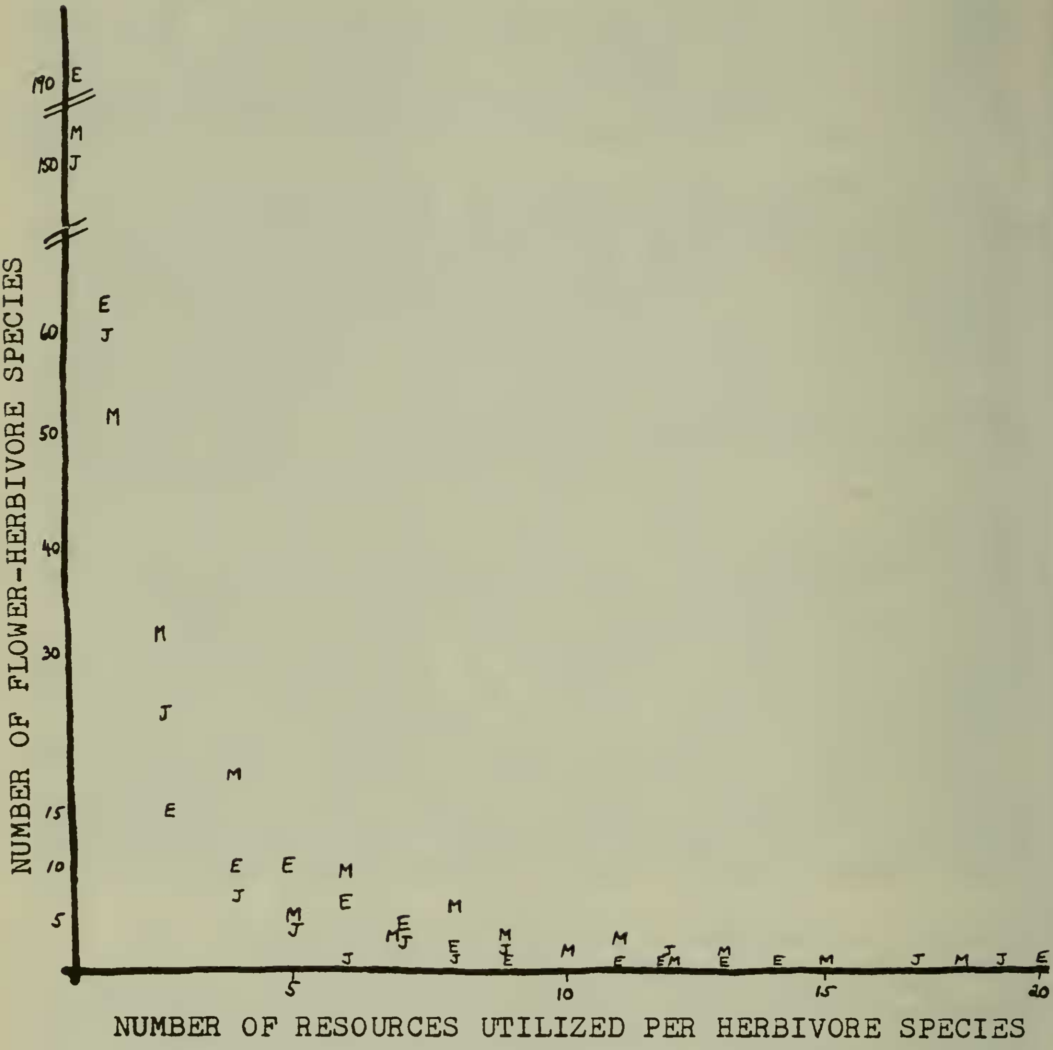


FIGURE 2. Number of resource plants utilized by Mediterranean scrub flower-herbivores.

E = Echo Valley mature chaparral
J = Japatul Valley burned chaparral
M = matorral of Fundo Santa Laura

bees is typically a relative phenomenon and thus the complete host range of a given bee species is essential for a knowledge of its degree of specialization. The degree of specificity observed at any point site may simply reflect the absence of certain plant taxa within the acceptable host range of the bee species or may be the outcome of competitive exclusion by sympatric nectar and pollen feeding species. In an attempt to deal with this problem, this study has entailed the observation of bee feeding habits at localities other than the established transect sites as well as extensive museum reference and correspondence with bee biologists (Moldenke and Neff, 1974a, 1974b).

Preliminary findings from these ongoing studies make it clear that the majority of the bee species of both Chile and California are indeed specialist feeders upon a particular genus, family, or similar limited array of closely related plant taxa. In the Pacific Coast and Sonoran Desert of the United States, there are nearly 2,000 species of bees, of which nearly 60 percent or 1,200 species are specialized feeders. However, of these 1,200 specialists at least 950 frequent taxa of only about 45 plant genera (Moldenke, 1979).

In other words, a one-to-one bee/plant relationship is rarely observed in nature. Rather there is tremendous overlap in the host preferences of specialist bees. It is pertinent to note that, while in many cases the relationship between floral host and specialist bee is indeed that of plant/primary pollinator (Hurd _et_ _al_., 1971; MacSwain _et_ _al_., 1973), this does not hold true in all cases. A plant which has "coevolved" with one specialist flower visitor commonly has not just one, but many species of specialist bees associated with it and is normally visited by numerous generalist taxa as well. Furthermore, in many instances, particularly those involving the numerous small specialist bees (3-6 mm body length), the bees are highly host specific and yet appear to be largely ineffective as agents of cross-pollination of their host plant due to such reasons as failure to contact the stigma, limited flight range and paucity of movements between individual plants (as opposed to intra-plant movement). While the factors which permit and maintain host specificity in bees are as yet poorly understood, a primary factor may possibly be the differing compositions of pollen (Vivino and Palmer, 1944), their relative nutritional values for solitary bees (Levin and Haydak, 1958) and the morphological specializations of the bees which presumably increase foraging efficiency (Linsley and MacSwain, 1958).

The majority of the flora must therefore rely on generalist bees or other flower frequenting groups for cross-pollination. This same phenomenon is apparent in Chile where we estimate that about 50 percent of the specialist bee taxa are primarily associated with about a dozen genera of plants.

In both countries both the number of specialist bee taxa and the percentage of specialist feeders in the total bee fauna increases with aridity (Moldenke, 1979). In the desert scrub communities 62 percent of the plant taxa that rely upon bee pollination have coevolved with specialist taxa, whereas 50 percent of the Mediterranean scrub and deciduous forest flora relying on bee pollination have specialists and a mere 25 percent of the coastal bee-pollinated flora possesses specialist vectors (Tables 4 and 5).

Resource utilization patterns of halictine bees in analogous communities provides another instance of convergent evolution of bees in the two continents. The halictines, a cosmopolitan group comprised of numerous small-to-medium sized species, are noted for their wide range of steps of social organization and the virtual absence of oligolecty or floral host specialization. The halictines in our study sites are generalists; while at any point in time individuals of a given species may show a marked preference for some particular plant species (commonly the plant producing the most abundant floral resources available in the community at the time), these preferences may change rapidly through the flowering season as different taxa come into bloom and other floral herbivore groups initiate or cease activity. As one might expect for such a generalist forager, these halictines generally lack the complex specializations of the feeding and pollen collection and transport systems so typical of specialist bees (Linsley, 1958). The generalist strategy the halictines pursue would appear to be most advantageous in situations where there is a rapid turnover of dominant flowering taxa through the flowering season.

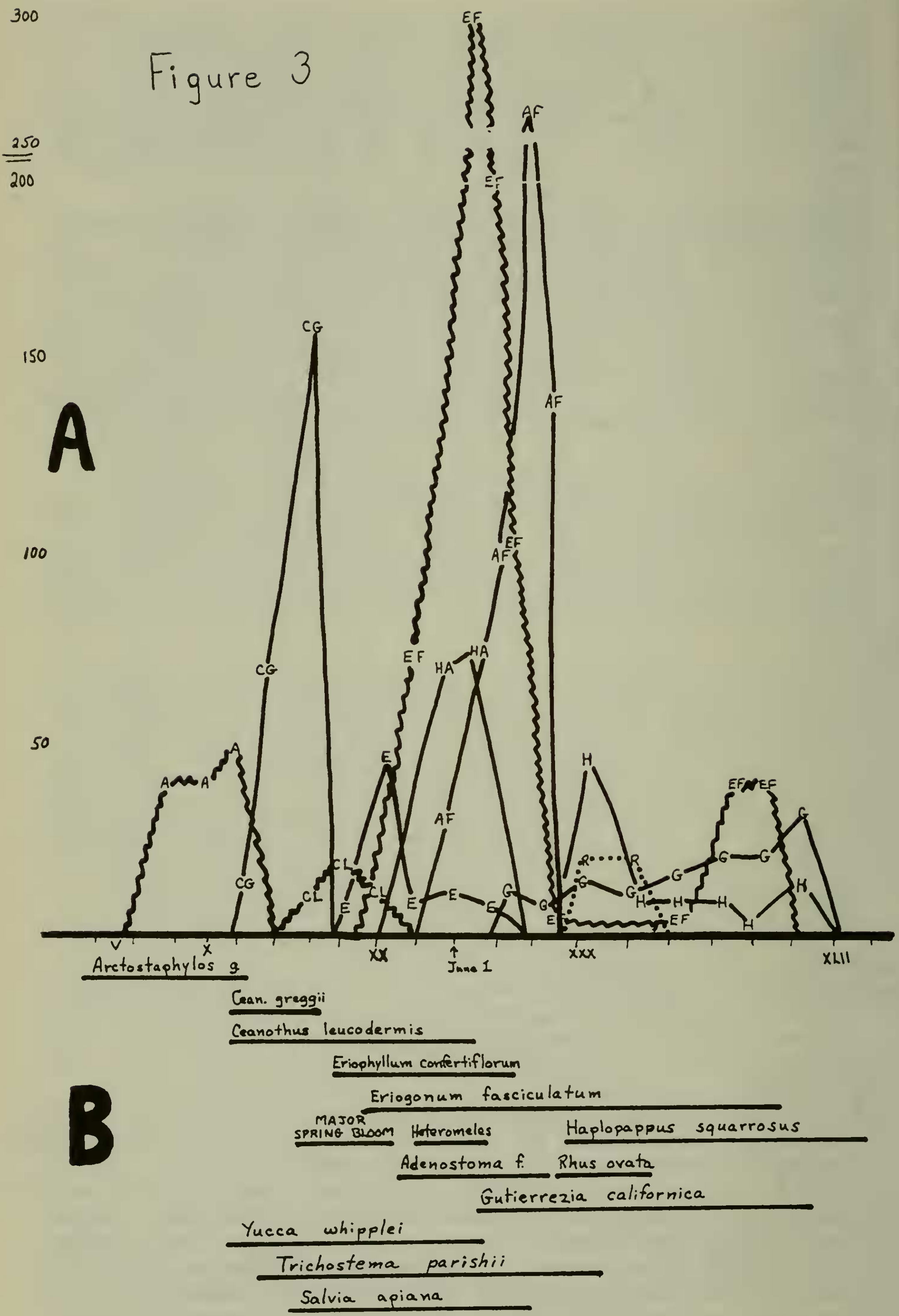
The Mediterranean scrub floras of both hemispheres have to a certain extent evolved the characteristic of non-overlapping flowering periods to insure minimum levels of pollen miscegenation (Mooney, 1972); only deep-rooted woody species capable of utilizing sufficient water throughout the dry summer can successfully compete by this mode. Figure 3 shows that all of the dominant perennials in the California site bloom at least in part either before or after the general blooming peak of all species and eight are capable of blooming after June 15th, by which time drought conditions are pronounced. Three of the four dominant species which do overlap the blooming peak to the greatest extent are not primarily bee-pollinated, possessing exclusionary morphologies adapted to moth(2) and hummingbird(1) pollination and are unavailable to halictine bees in general. All of the other dominant plant species (with the possible exception of *Arctostaphylos*) are conspicuously mass flowering taxa with inforescences of small specialized flowers, unlike most temperate North American communities where anemophily dominates. Semisocial halictine bees are very efficient pollinators in this habitat (especially in Chile) because they are able to utilize each of the shrub bloomers in succession throughout the blooming season (Figure 3). The flowers of the dominant species of the Mediterranean scrub community are structurally relatively similar and thus do not require morphological specialization as a prerequisite for efficient foraging on any particular species. In the compressed blooming season of the desert, on the other hand, competition among both annual and perennial plants for specificity of pollen transfer has led to a contemporaneous array of dissimilar floral morphologies (Simpson 1977; Simpson *et al*, 1977).

In the coastal scrub, where floral herbivores of all types are scarce, the halictines are not particularly diverse; yet they are the dominant pollinators for twenty-five percent of the bee-pollinated flora. A similar percentage (22%) of the bee-pollinated flora of the Mediterranean scrub relies upon halictines for pollination. In contrast, only two to three percent of the bee-pollinated flora relies upon the halictines as their primary pollinators in the temperate forests, where flowers tend to be widely scattered and the dominant mass bloomers are anemophilous, and in the desert, with its unpredictable yet strongly weather

FIGURE 3. Seasonal resource utilization by halictine bees in the mature chaparral at Echo Valley. (excludes the very poorly known *Halictus harmonius* found on *Adenostoma* and *Eriogonum* in large numbers at this site)

A) Relative abundances of all halictines on the dominant resources from weeks VI to XLII of study. Note that three dominant species are unvisited by halictines.
B) Periods of peak anthesis of the dominant shrub species; periods of scattered blooming are not included. Note that *Eriogonum* is not a preferred resource for much of its period of anthesis. The period of the major spring bloom, from April 1 to May 15, is also indicated.

Figure 3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June 1
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Arctostaphylos g.
Cean. greggii
Ceanothus leucodermis
Eriophyllum confertiflorum
Eriogonum fasciculatum
MAJOR SPRING BLOOM
Heteromeles
Haplopappus squarrosus
Adenostoma f.
Rhus ovata
Gutierrezia californica
Yucca whipplei
Trichostema parishii
Salvia apiana

controlled patterns of alternating dearth and abundance of flowers (Tables 4 and 5).

Feeding specialization is especially pronounced in the desert regions of both continents. Sixty-three percent of the total bee fauna in the California deserts are probable or apparent specialist feeders (Moldenke, 1976). In Chile feeding specialization information is more imprecise, but 59 percent of the presently recognized desert taxa are apparently specialist feeders. The Chilean deserts have not been extensively collected for insects, and the species still to be described will probably increase this percentage still further. Generalist-feeding desert bees which are abundant in the deserts of Catamarca, Argentina (e.g. Centris spp; Neff unpub. data) are not present in significant numbers in either Chile or California. In the western extremes of the deserts of the two continents, rainfall is lowest and least predictable, a situation which favors the specialist flower visitors which are utilizing precise environmental cues to emerge synchronously with their particular host plant.

In the cooler and moister temperate forests and immediate coastal environments, the blooming period of individual plants as well as the whole blooming season is protracted and less selective advantage rests with precise synchronous emergence times. Flower-herbivores of all types decrease as the temperature drops and generalist feeding heterothermic bumblebees become the major flower visitors and pollinators in all but the densest forest types. On the transects reported herein, bumblebees are nearly absent (one rare species observed in both continents), but 500 miles poleward in each continent they comprise more than 50 percent of the flower visitor individuals and more than 95 percent of the total flower-herbivore biomass. Specialist solitary bees are nearly absent in these climates, and the bulk of other vectors are generalist-feeding muscoid flies and halictine bees.

f) Feeding Overlap of Sympatric Specialists

A discussion of the species diversity and resource utilization patterns of flower-herbivores in Chile and California must analyze distributional patterns and niche overlap. Studies in California (Moldenke and Neff, 1974a, 1974b; Moldenke, 1971, 1976) have shown that bee species usually show a remarkable degree of fidelity to habitat type, the exception being high altitude Sierra Nevada communities where β-diversity is extremely low. Although data for other groups is not as good, this fidelity apparently is characteristic of pollinating taxa in general. The most obvious feature of bee distribution in Chile (Moldenke and Toro, in prep. is the exceedingly wide habitat and altitudinal tolerances exhibited by most Chilean bees. Frequently the same species occurs in a coastal region, a matorral locality and at 3,000-4,000 m in the Andean Cordillera. Often species are distributed from the secondary growth in the temperate forests of southern Chile (Valdivia, latitude 40° S) throughout all altitudes and most intervening community types to the edges of the Atacama Desert (latitude 29° S). Rather than a habitat or altitudinal replacement of species, which is the general rule in California, the general pattern in Chile is replacement with large changes in latitude.

This observation sheds considerable light on the pattern of resource utilization and sympatry of closely related competitors between the two regions. In California large numbers of congeneric, sympatric, specialist-feeding taxa are often found on the same host plant. For example, ten very closely related species of *Perdita* (*Heteroperdita*) are specific to *Coldenia* at the Ocotillo desert scrub site (Timberlake, 1954 and unpub. obs.) and nearly all the described species (18) of *Proteriades*, a specialist on *Cryptantha*, occur on the same species at Riverside, California (Timberlake and Michener, 1950). Our studies (Moldenke and Neff, 1974b) at the California sites frequently documented instances of 4-10 congeneric specialists utilizing the same host plant. In Chile, however, even though there are many specialist-feeding taxa and many have coevolved with the same resource genus, our studies (Moldenke and Neff, 1974b) show very few examples of sympatric congeneric specialists within any localized research site. (Two instances of three congeneric specialists on the same Chilean pollen plant are the only notable examples.) The factors controlling the distribution and co-occurrence of Chilean bees are even less well-delineated than the corresponding ones for California bees. However, in this regard the differing effects of Pleistocene glaciation in the two regions play a significant role. The lack of large refugia for the Chilean fauna and the considerable contraction of an already geographically limited inhabitable region must have led to widespread faunal extinction Competition during pluvial periods must have been most severe between congeneric specialists since they presumably differed less in their requirements than did specialist competitors in differing genera. The present interpluvial pattern of species distributions reflects the recolonization of large regions of expanding semiarid vegetation (as the forests recede to the south) by the depauperate fauna that survived the intense competition. In the arid portions of North America, pluvial periods had the effect of fractionating continuous distribution patterns. Though the total arid and semiarid area may have shrunk, it never decreased to the proportions that must have occurred in Chile. The imposed patchiness of distribution patterns presumably has led to the rate of speciation evidenced in California. Present patterns of sympatry may represent subsequent reinvasion of the now continuous widespread semiarid conditions.

CONCLUSIONS

The basic thrust of my recent research has been to determine the variety of interactions in the interface between flowering plants and flower-feeding herbivores. In all, five series of clinally related community analogues have been studied in order to elucidate the patterns at a community level (Moldenke, 1975; Moldenke and Lincoln, 1979; Neff, unpub.). The methodology has been designed to analyze both the manner in which diverse taxonomic groups of herbivores utilize the available floral resources in the different communities and the manner in which the flowering plants partition the potential pollen vectors. The parameters such research has begun to quantify are: the degree of specialization of interacting plant and animal species; the relative importance of buffered interactions within trophic pyramids in terms of the number of generalist flower feeders and the number of plant species pollinated by many vector taxa; and the degree of redundancy built into the food web by the interactions of taxonomically different but energetically or ecologically equivalent species.

Studies along an altitudinal transect of fifteen community types across central California (Moldenke, 1971, 1975), have demonstrated that:

1) Total species number of flower herbivores increases with stability and predictability of the climate.

2) Niche-specialization as a strategy is progressively more successful in terms of total number of species and total individuals of both plants and flower visitors as the climate ameliorates.

3) The percentage (by species count) of highly specialized species of both plants and flower-feeding herbivores increases in the most severe environments at the expense of the more moderately specialized species; however, the vast bulk of the individuals and trophic energy flow are attributable to a few extremely

abundant supergeneralist species.

4) Energetic flow chart redundancy attributable to distinct species of herbivores which feed on overlapping food resources increases in extreme environments. This increase in generalists is especially noticeable in terms of relative biomass and abundance of individuals and occurs most notably at the expense of moderately but not highly specialized species.

5) Similar physiognomic communities at widely different geographical localities are in most cases much more similar in terms of their pollination systems and the feeding habits of their respective pollinators than different community types at a given geographical site.

All of these results are commensurate with the hypothesis that, while there is a tendency towards specialization in most environments, it is only in the most predictable or stable environments that the loss of both behavioral and genetic flexibility resulting from specialization is a viable strategy. However, in the most extreme environments (alpine and desert), behavioral feeding specialization may occur and be a necessary prerequisite permitting the existence of ephemeral populations which thrive briefly but frequently must recolonize following local extinctions brought about by the severe unpredictability of these environments.

Results cited in this report not only substantiate the pattern previously recorded in California but further demonstrate that:

1) Total species number and diversity trends are directly correlated to similar climatic conditions in both continents;

2) Emphasis is on niche-generalists in maritimal and Mediterranean scrub environments in terms of relative species numbers;

3) Emphasis is on niche-generalists in terms of total number of individuals in the Mediterranean scrub environment;

4) Feeding specialists are the major adaptive life-style in the desert;

5) As one travels poleward along the Pacific coasts of both continents, flower-feeding generalists represent nearly all the biomass and virtually all the significant energy flow in both the maritime and forest environments.

The basic components of competitive species interactions have indeed resulted, at the local level in both continents, in the convergent evolution of similar species diversity, similar gross efficiency (relative biomass of flower-eating herbivores supported) and cross-link patterning of this section of the community food web.

Two further basic tendencies in convergent evolution which are manifest in this intercontinental site comparison indicate the possibility of generalizing the results to other sections of the world:

1) On a world-wide scale bee speciation has occurred at an extremely high frequency under certain climatic regimes (Linsley, 1958). The semiarid/arid regions of the southwestern United States, central Chile, South Africa, northern coast of Africa and parts of Australia support very rich bee faunas (Linsley, 1958). (California = nearly 2,000 species; Chile = 500, probably 700 when northern regions are fully explored -- contrast these figures to 65 species for southern Florida (Graenicher, 1930) and only 356 for Panama and adjacent Central America (Michener, 1954) -- two regions with non-anemophilous floras more diverse than those under consideration in this report even though they are smaller in area and contain less topographic heterogeneity.)

2) The floras of Chile and California are well known to be quite diverse, considering latitude and geographical extent. Geographically, both regions contain a remarkable amount of varied relief, which has facilitated rapid evolution of a relatively large flora, characterized in both instances by a heavy emphasis on annual species (about 50 percent of total, or at least three times the world average; P. Raven, pers. comm.). Annual plants are often characterized by synchronized blooming, short life cycles, emphasis on evolved genetic self-compatibility and facultative inbreeding. Therefore the diversity and distribution of resources through space and time are roughly equivalent in the opposing continental sites.

The conclusions drawn from the California/Chile research corroborate in general that it is the over-all climatic characteristics which determine plant phenology and structure, which in turn limit and define the emphases of different strategies of resource utilization (Cody, 1974; Schoener, 1972). Equally important, however, are the observations of non-correspondence. Most importantly though, other ecological subunits of the community may show one-for-one or two-for-one species correspondence in the two hemispheres (Mooney, 1977), whereas the species-rich nature of appropriate pollinator guilds (not defined in the present paper in other than the broadest taxonomic terms) precludes this type of comparison or species-for-species analysis. That a significant difference in such species packing phenomena does occur, is seen in the near absence of congeneric bee species utilizing the same resource in common in Chile, as is the distinctly higher values of species richness found throughout all the North American sites relative to their Chilean analogues.

Procedurally paramount is the role exerted by the fire in chaparral/matorral. Even though on a total floristic basis both Mediterranean regions are characterized by very diverse annual floras, in Chile the annual and shrub floras are apparently synchronous, whereas in California annual plants are nearly absent from mature chaparral. Because the fire succession is a very short one in California and the extent of precolonial natural fires was supposedly very limited, I feel that it is procedurally more equitable to combine both parts of the California cycle for comparison with the matorral. The presence of a cycle in California is a distinct lack of convergence, however, and for some aspects of the communities which are not suitably additive in this manner analysis of convergence becomes moot. An additional important lack of convergence in evergreen sclerophyll scrub is the pronounced diversity of the dominant shrubs of Chilean matorral.

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